

## III. BIOENERGETIC SPECTRA OF SKIPJACK AND YELLOWFIN TUNAS

*James F. Kitchell*

*William H. Neill*

*Andrew E. Dizon*

*John J. Magnuson*

## A. Introduction

A major research facility devoted to the study of captive tunas (Nakamura, 1972) has provided some opportunity to develop greater understanding of the biology of the skipjack tuna (*Katsuwonus pelamis*). Evidence to date indicates remarkable adaptation to pelagic environments and an unusual physiology associated with life in relatively warm but unproductive waters (Brock, 1974; Magnuson and Heitz, 1971; Magnuson, 1973; Stevens and Neill, in press). Remarkable features of skipjack tuna biology include (a) obligatory continuous swimming associated with the absence of a gas bladder (Magnuson, 1973) and lack of respiratory pumps (Brown and Muir, 1970); (b) warm-bodiedness owing to retention of metabolic heat via countercurrent heat exchangers in the blood-vascular system (Stevens and Fry, 1971; Stevens, Lam, and Kendall, 1974; Neill, Chang, and Dizon, 1976); and (c) activity-dependent respiration rates that appear independent of both ambient temperature (Gordon, 1968) and the allometric effect of weight (Gooding and Neill, ms).

All the tunas are extremely difficult to maintain for experimental work. Because animals often die shortly after handling (e.g., following weight determination), studies are limited in scope and duration. Nonetheless, recent and ongoing work (Neill et al., 1976; Sharp and Francis, 1976; Kitchell, Magnuson, and Neill, 1977; Gooding and Neill, ms; Uchiyama and Strusaker, ms; Barkley, Neill and Gooding, ms) has provided data and concepts that permit establishment of a hypothetical yet holistic framework for future research on tuna bioenergetics.

In this paper, we attempt to combine principles of bioenergetics with data from experimental and field studies to construct energy budgets for skipjack tuna and thereby define this scombrid's scope for growth (Warren, 1971). Using data of Sharp and Francis (1976), the analysis is then extended to yellowfin tuna (*Thunnus albacares*). Our goal in this effort has been a more coherent characterization of the growth process

in tunas and identification of those physiological, behavioral, and/or ecological processes that have the greatest potential for improved understanding of tuna biology.

#### B. Energy Budget Components and Their Units

Using conventional symbol notation (Ricker, 1971), the mass balance or energy budget equation may be written

$$C = R + U + F + G + \Delta B \quad (1)$$

where

- C = rate of food consumption
- R = rate of metabolism (respiration)
- U = rate of excretion
- F = rate of egestion
- G = rate of gamete production
- $\Delta B$  = rate of growth

Our handling of budget terms has necessitated subdivision of R into two component parts:

$$R = SDA + M ,$$

where SDA (specific dynamic action) is the rate of energy cost associated with processing the input energy source (mainly, deamination of proteins) and M is the rate of energy expenditure associated with the remainder of metabolic work, or net metabolism (basal metabolism and activity).

Each term in the equation may be defined in biomass equivalents in developing mass-balance solutions. Because the caloric functions as the common denominator in bioenergetics (Warren, 1971), the equation may also be written in caloric units if energy equivalents are known for biomass units and catabolic processes.

To facilitate calculations, all parameter estimates are given in per day units based on a sexually immature 1 kg (live weight) skipjack tuna at 24°C. Caloric values for skipjack biomass are 1.46 kcal/g live weight (Kitchell et al., 1977). Although food habits of skipjack are highly variable (Yuen, 1959; Manar, 1966; Magnuson and Heitz, 1971), volumetric composition approximates 50% invertebrates and 50% fishes; we estimate these to have caloric equivalents of 1.0 kcal/g wet weight and 1/2 kcal/g wet weight, respectively. Thus, mean caloric value of skipjack forage is taken as 1.1 kcal/g wet weight.

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### C. Energy Budgets for Skipjack Tuna at Six Input-Output Regimes

In this section, we attempt to evaluate the energetics spectrum of skipjack tuna by determining energy budgets at six levels--starvation, maintenance (no weight change), observed growth at three levels of metabolism, and estimated maximum daily ration.

1. Starvation. Lacking any input, energy loss results from (a) metabolic demand; and (b) secretions and excretions. Gooding (Southwest Fisheries Center, National Marine Fisheries Service, Honolulu, personal communication) measured routine oxygen consumption at 24°C for fasted skipjack tuna weighing 0.63 to 3.90 kg. The resulting regression equation was  $Y = -0.340 + 0.016X$  ( $n = 40$ ), where  $Y = \log_{10}$  mg  $O_2$  consumed per g fish per hour and  $X = \log_{10}$  (weight of skipjack, g). Both the basal rate and the weight exponent are substantially greater than those reported for most fish species (Gordon, 1968; Beamish and Dickie, 1967). Using an oxycalorific equivalent of 3.4 cal mg  $O_2^{-1}$  (Warren, 1971), routine daily metabolic output of a fasted 1 kg skipjack tuna would be 510 mg  $O_2 h^{-1} \times 3.4 \text{ cal mg}^{-1} \times 24 \text{ h day}^{-1} = 42 \text{ kcal day}^{-1}$ . Brett (1971) and Warren (1971) estimate that  $O_2$  consumption measures only 80% of total energy loss associated with mobilizing body tissues for metabolic activity. The remaining 20% is lost both as heat associated with deamination of protein and excreted nitrogenous waste. The former is termed specific dynamic action (SDA) and accounts for approximately 15% of the total output, while the latter is largely ammonia and/or urea containing about 5% of initial energy content. Accordingly, total energy output would be the sum of SDA and calories excreted as metabolic waste products. Empirically,  $42/0.8 = 53$  kcal of total energy output fish $^{-1}$  day $^{-1}$ . The energy content of the whole fish is 1,460 kcal; therefore, the rate of loss would be  $53/1,460 = 36 \text{ cal kcal}^{-1}$  or about 3.6% of total energy content per day (Table I). For a skipjack swimming at or near its minimum speed ( $V_{100}$  of Magnuson, 1973), the weight-specific equation for routine metabolism in caloric units becomes  $M = 29W^{0.016}$  where  $M = \text{cal kcal}^{-1} \text{ day}^{-1}$  and  $W = \text{fish weight in kilograms}$ .

Because fish utilize high-energy tissues (e.g., fat) and hydrate when starved, weight loss alone is an underestimate of net change in energy (Brett, 1973; Niimi and Beamish, 1974; Kitchell et al., 1977). Skipjack lost about 1.8% of body weight per day (Dizon, Southwest Fisheries Center, Honolulu, personal communication) during the first 25 days of a starvation period. Data from Kitchell et al. (1977) indicate change in energy content per unit weight of about 1.8% per day

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TABLE I. Estimated Energy Budget Terms at Six Bioenergetic Regimes for a 1 kg Skipjack Tuna at 24°C<sup>a</sup>

Bioenergetic regime	Requisite ration (% body wt. day <sup>-1</sup> )	Process rate (cal kcal <sup>-1</sup> day <sup>-1</sup> )					
		Con- sumption (C)	Net Me- tabolism (M)	SDA	Excre- tion (U)	Eges- tion (F)	Growth (ΔB)
Starvation	0	0	29	5	2	0	-36
Maintenance	5.9	44	29	7	2	7	0
Observed growth at							
1 Lab M (= Level I)	7.3	57	29	9	3	9	7
2 Lab M (= Level II)	13.1	99	58	15	5	15	7
3 Lab M (= Level III)	19.0	143	87	21	7	21	7
Maximum	30.0	250	87-155	38	12	38	7-69

<sup>a</sup>Daily ration is given as percentage of body weight consumed per day assuming 1.1 kcal per gram live food.

for skipjack starved 10 days. Combining absolute weight changes with changes in caloric density yields an independent estimate of  $1.8 + 1.8 = 3.6\%$  loss per day, exactly the value determined from the balanced energy budget.

2. *Maintenance.* Calculation of a maintenance ration must include outputs proportional to feeding level as well as routine metabolic rate. Although experimental data which would provide measures of rates of excretion, egestion, and SDA for skipjack tuna are not available, we can estimate these rates based on studies with other fishes.

Excreted energy includes by-products and wastes, such as ammonia and urea, resulting from deamination of consumed protein. Caloric output is generally taken as 3% to 7% of consumed calories (Winberg, 1960; Mann, 1967). Using a mean of 5%, we estimate excreted energy, U, as a constant proportion of consumption rate, C; thus,  $U = 0.05C$ .

Egestion or fecal output can be similarly estimated as a constant proportion of consumption; existing studies of carnivorous fishes indicate that absorption efficiencies are not strongly related to feeding level (McComish, 1970; Kelso, 1972). Of the calories consumed as invertebrate foods we estimate that 20% would be egested (McComish, 1970), whereas as little as 10% of calories consumed as fish would be egested (Kelso, 1972). Using a mean of egested calories, we estimated  $F = 0.15C$  for the mean diet.

As described above, the specific dynamic action component of energy output, SDA, is broadly defined as the energetic cost of converting food for catabolic and/or anabolic processes

(Warren, 1971). Based on the experimental data of Muir and Niimi (1972) and Beamish (1974), we estimate that 15% of consumed calories are expended as heat in SDA; thus, SDA is set equal to 0.15C.

Using the measured value of routine metabolism for a fasted fish, substitution in equation 1 yields

$$C = (42 + 0.15 C) + 0.05 C + 0.15 C + 0 + 0 ;$$

therefore,

$$0.65 C = 42 ; \quad (2)$$

$$C = 65 \text{ kcal fish}^{-1} \text{ day}^{-1} ;$$

and,

$$C/1,460 = 44 \text{ cal kcal}^{-1} \text{ day}^{-1} .$$

In biomass units, a 1 kg fish must consume 65/1.1 (assuming a mixed diet) = 59 grams of food for a maintenance ration of 5.9% of fish weight per day (Table I). This estimate of maintenance is derived for fish swimming at or near their minimum speed in a respirometer, and should not be construed as representative of the minimum energy requirements of fish in nature. Note, however, that the maintenance ration for skipjack tuna is equivalent to or greater than the maximum ration for most nonscombrid fishes of equivalent size (Magnuson, 1969).

3. *Observed Growth at Three Levels of Activity.* Mann (1967) described the assumptions of what we call the Winberg approach (Winberg, 1960), which has been widely applied in fish energetics studies (see Backiel, 1971; Healy, 1972; Burbidge, 1974; Ware, 1975). Briefly restated, the routine metabolic rate determined in a respirometer is doubled to estimate metabolic levels for most fishes under natural conditions. More recently, Ware (1975) estimates that a three-fold increase might be more appropriate for applications to pelagic fishes. Bioenergetic studies of terrestrial vertebrates employ a similar 2-3x multiplier for field applications (Brody, 1945; Dutton, Fitzpatrick, and Hughes, 1975).

To estimate an energy budget for normally growing, minimally active (Level I) skipjack tuna, we combined parameters of a maintenance budget with an observed growth rate of 0.7% in weight per day for 1 kg skipjack as calculated from growth curves (Uchiyama and Struhsaker, ms) and length-weight relations (Magnuson, 1973). Growth is equivalent to  $0.007 \times 1,460 \text{ kcal} = 10 \text{ kcal fish}^{-1} \text{ day}^{-1}$ ; thus the budget equation is

$$0.65 C = 42 + 10$$

$$\text{or } C = 80 \text{ kcal fish}^{-1} \text{ day}^{-1} .$$

The daily ration would be  $80/1.1 = 73$  gram food per 1 kg fish or about 7.3% per day for  $0.7\% \text{ day}^{-1}$  growth in weight or a gross growth efficiency of about 10% (Table I).

By assuming that higher levels of activity in nature result in a twofold increase in routine metabolic rate (Level II), the equation becomes

$$0.65 C = 2(42) + 10$$

$$\text{or } C = 145 \text{ kcal fish}^{-1} \text{ day}^{-1},$$

which converts to a ration of 13.1% per day. Assuming a three-fold increase in routine metabolism (Level III) yields  $C = 209$  kcal per fish or a daily ration of approximately 19.0% (Table I). Gross growth efficiencies would be 5% and about 4%, respectively for the higher activity levels.

4. *Maximum Input-Output of Energy.* To evaluate this energy budget we set the input parameter,  $C$ , to its maximum, calculated outputs, and compared the results with those determined independently from observation or experimentation. When combined with known metabolic rates or maintenance rations, the scope for growth is delineated as defined by Warren (1971).

Digestion rate and relative stomach volume intrinsically limit rates of food consumption. Within a species both are inversely related to fish size. As a result the maximum daily ration,  $C_{\max}$ , declines allometrically with weight,  $W$ , and may be written as  $C_{\max} = aW^{-b}$ .

Based on previous *ad libitum* feeding studies using whole fish as food (Magnuson, 1969), the maximum daily ration of a 1.5 kg skipjack was estimated as 15-20%. Recent studies by Steffel (Southwest Fisheries Center, Honolulu, personal communication) indicate that smaller food particles are more readily consumed and that maximum rations for 1.4 kg skipjack are approximately 28-35%. Using a value of 30% and converting to caloric units assuming natural foods, estimated consumption would be 330 kcal total or about 225 cal  $\text{kcal}^{-1}$  biomass  $\text{day}^{-1}$ . The value of the weight exponent,  $b$ , is not available for skipjack but may be estimated as -0.3 based on results for other fishes (Brett, 1971; Niimi and Beamish, 1974; Kitchell et al., 1974). Taking  $b$  as -0.3 and then estimating  $a$  from Steffel's data yields an estimated  $C_{\max}$  of 250 cal  $\text{kcal}^{-1}$   $\text{day}^{-1}$  for 1 kg skipjack ( $C_{\max} = 250 W^{-0.3}$ , where fish weight,  $W$ , is in kg).

Energy outputs as specific dynamic action (SDA), excretion ( $U$ ), and egestion ( $F$ ) are constant proportions of consumption representing a loss of 35% of calories consumed. Thus, energy available for net metabolism, growth, and (in larger fish) gamete production would be  $0.65 C_{\max}$ . Limits described by these equations are given as a function of fish weight (Fig. 1).

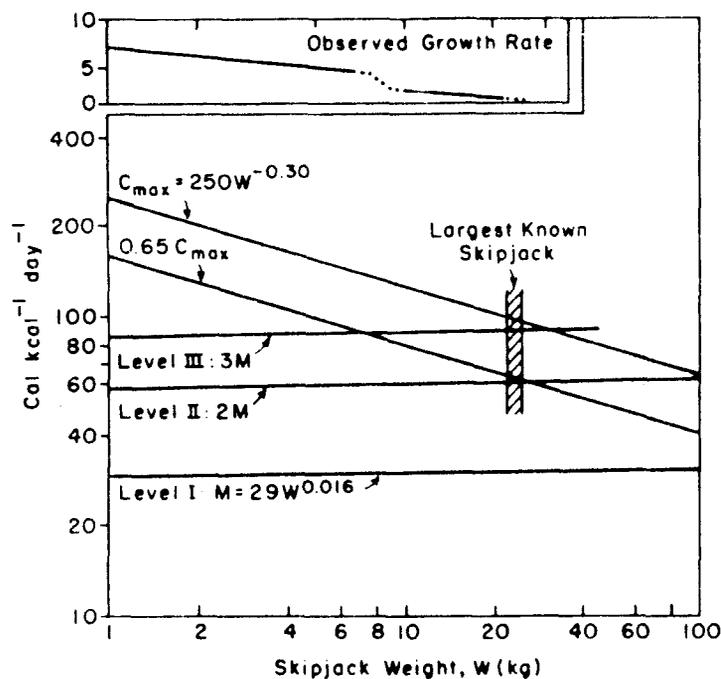


FIG. 1. Relationship of estimated maximum caloric intake and outputs to size of skipjack tuna, *Katsuwonus pelamis*. Parameters and symbols are described in text.

Based on otolith analysis (Uchiyama and Struhsaker, ms), the daily growth increment of skipjack tuna appears to be a nearly linear function of log (weight). Skipjack growth includes energy stored in both somatic growth ( $\Delta B$ ) and gonadal development ( $G$ ). Subtracting observed growth from  $0.65 C_{\max}$  gives an estimate of the energy available for net metabolism. Also plotted in Fig. 1 are the presumed lower (Level I) and upper (Level III) limits of net metabolism as multiples of routine metabolism determined by Gooding and Neill (ms) from captive fish.

Interpretation of Fig. 1 should be made with caution. First, weight-related rate functions are extrapolated from data gathered for small (0.6–4.0 kg) skipjack. Second, no basic physiological or ecological criteria truly justify expressing metabolic rates as multiples of the routine rate. This practice simply serves to characterize relative levels of activity estimated to occur under natural conditions.

#### D. Limits on Growth and Maximum Size of Skipjack Tuna.

Differences between rates of maximum energy intake and estimated energy costs (Fig. 1) allow an estimate of bioenergetic limits on growth rate. For example, a 1 kg skipjack feeding at the maximum rate and maintaining a metabolic rate approaching Level III would process  $0.65 \times 250 = 162 \text{ cal kcal}^{-1} \text{ day}^{-1}$  of which  $3 \times 29 = 87 \text{ cal kcal}^{-1} \text{ day}^{-1}$  would be metabolized, leaving  $25 \text{ cal kcal}^{-1} \text{ day}^{-1}$  for growth. The observed growth rate is approximately  $7 \text{ cal kcal}^{-1} \text{ day}^{-1}$ . If wild skipjack do maintain Level III metabolism, individuals smaller than about 7-10 kg are growing at rates substantially less than maximal. As noted by Ware (1975), active metabolic rates are probably not greater than threefold routine rates. Thus, smaller animals appear limited by food availability and/or their efficiency as predators.

Growth of skipjack larger than 7-10 kg appears limited not by the availability of food but by the maximum rates at which available food can be physically consumed and physiologically processed. This limitation becomes increasingly important as the fish grow larger (Fig. 1). Level III metabolism cannot be sustained in skipjack larger than about 8 kg; at about 25 kg, even Level II metabolism requires more energy than can be provided by  $C_{\text{max}}$ . We propose that maximum size in skipjack tuna reflects the point of balance between the minimum rate of energy expenditure consistent with normal activity and the maximum rate of energy acquisition ( $C_{\text{max}}$ ), the latter governed largely by factors intrinsic rather than extrinsic to the fish.

Under an assumption of model (Fig. 1) validity, it becomes a simple matter to predict maximum skipjack size given the rate of metabolism at maximum size or, conversely, to predict the normal rate of metabolism in a skipjack of maximum size. The second prediction is the appropriate one because we have from independent sources a good estimate of maximum size in skipjack, but no estimates at all of rates of energy expenditure in wild tunas.

The largest skipjack tuna on scientific record weighed 22 kg (Magnuson, 1973); larger (>25 kg) skipjack are rumored to have been caught. According to our model (Fig. 1) the no-growth point for a 22-kg skipjack tuna eating its maximum daily ration occurs at a level of metabolism slightly more than twice the routine rate extrapolated from laboratory data. While this prediction conforms with Winberg's (1960) conclusion that the mean metabolic rate of fish in nature is about twice the routine rate, its accuracy cannot be judged on the basis of existing data.

In typical fishes, maximum size appears limited not by the size of  $C_{\text{max}}$  but by progressive inability of fishes to

consume at the  $C_{max}$  rate--the energy cost of obtaining  $C_{max}$  becomes greater than the energy return from  $C_{max}$  (Weatherly, 1972). One must presume that this is because evolutionarily  $C_{max}$  has kept pace with (or a step ahead of) the average rate at which food is available for consumption. Why has this not, apparently, been the case for skipjack tuna? Perhaps because the bioenergetic strategy of skipjack tuna has been tempered by a peculiar consideration of no relevance in the evolution of typical fishes--a thermal "squeeze" in which skipjack larger than some critical size risk overheating their core tissues at all environmental temperatures higher than the minimum temperature for function of superficial tissues. Under this hypothesis (Neill et al., 1976), the habitat available to skipjack tuna becomes progressively reduced as the fish grow larger, with larger fish restricted to the cooler part of the range habitable for smaller fish. Barkley et al. (ms) have extended the thermal-squeeze hypothesis to include an additional restriction imposed by low dissolved oxygen; their resulting model of skipjack distribution by size in the eastern and central Pacific seems reasonably consistent with fishery-catch data and with the apparent migration patterns of skipjack.

Under the assumption that normally active skipjack must maintain an average metabolic rate of  $3 \text{ mg O}_2 \text{ g}^{-1}\text{hr}^{-1}$  in their red muscle, Neill et al. (1976) suggest that the thermally tolerable habitat for skipjack vanishes as the fish approach 22 kg. A routinely active skipjack tuna has a red muscle metabolic rate of about  $1 \text{ mg O}_2 \text{ g}^{-1}\text{hr}^{-1}$  (Neill et al., 1976); thus, their assumption of a  $3 \text{ mg O}_2 \text{ g}^{-1}\text{hr}^{-1}$  rate for wild fish is equivalent to presumption that the normal wild rate is thrice the rate measured in routinely active captive animals. Trebling of red muscle metabolic rate is equivalent to doubling of whole-body routine rate if, as seems reasonable (Dizon, Brill, and Yuen, this volume), one-half the routine oxygen demand of the whole animal is attributable to red-muscle activity. In this sense, then, the present bioenergetic hypothesis and the thermal-squeeze hypothesis are consistent: they invoke equivalent metabolic rates to account for the observed maximum size of skipjack tuna. The thermal-squeeze hypothesis makes more tenable the unusual role of  $C_{max}$  as a limiting factor in growth to maximum size, for skipjack had nothing to gain evolutionarily by increased  $C_{max}$  if risk of overheating set limits on energy output at maximum size.

Skipjack energy budgets (Table I) and extrapolations (Fig. 1) were based on the rates calculated for a constant temperature of 24°C. Would a reduction in temperature with fish size, in keeping with the thermal-squeeze hypothesis, substantially alter the bioenergetic spectrum of skipjack? Probably not, because metabolism and activity in skipjack

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tuna appear virtually independent of environmental temperature (metabolism--Gordon, 1968; activity--Stevens and Fry, 1972; Dizon et al., in press; Chang et al., ms; Dizon, Brill, and Yuen, this volume).

#### E. Bioenergetic Limits for Yellowfin Tuna

Sharp and Francis (1976) estimated energy budget parameters for yellowfin tuna in the eastern Pacific. Beginning with Gooding and Neill's (ms) estimates of metabolic rate in skipjack tuna, they assumed that yellowfin metabolic weight was better approximated as  $W^{0.8}$ . Thus, the equation for routine metabolism of yellowfin became  $M = 29 W^{-0.2}$ , where  $M$  is in cal  $\text{kcal}^{-1}$  fish  $\text{day}^{-1}$  and  $W$  is fish weight in kilograms. Caloric density of yellowfin biomass was assumed to be similar to skipjack (Sharp and Francis, 1976). Consideration of calculated daily ration as a function of yellowfin weight (see Sharp and Francis, 1976: fig. 5) leads us to suppose that  $C_{\text{max}}$  (in cal  $\text{kcal}^{-1}$  day $^{-1}$ ) =  $190 W^{-0.35}$ . Therefore, the maximum rate at which energy is available for growth and net metabolism in the yellowfin is  $124 W^{-0.35}$  cal  $\text{kcal}^{-1}$  day $^{-1}$  (=  $0.65 C_{\text{max}}$ ).

As for skipjack (Fig. 1), now we can estimate relationships between metabolic levels, maximum available energy, and fish size for yellowfin (Fig. 2). The exercise leads to a conclusion identical to that reached above for skipjack tuna: maximum available energy and the energy required for metabolic

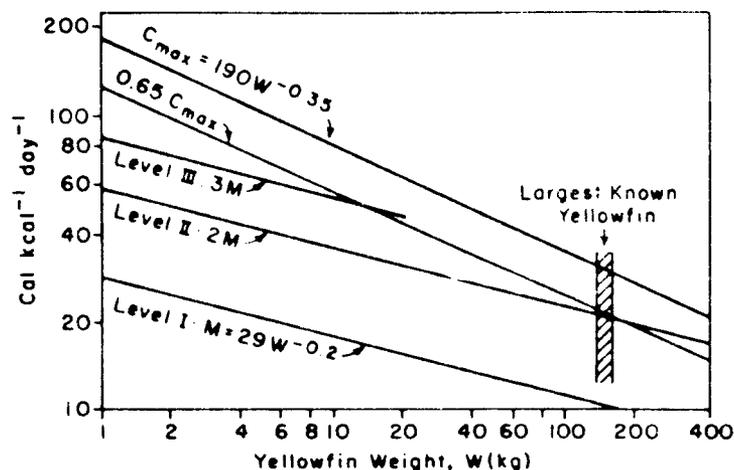


FIG. 2. Relationship of estimated maximum caloric intake and outputs to size of yellowfin tuna, *Thunnus albacares*. Parameters and symbols are described in text.

levels slightly in excess of twice the routine rate converge at a weight equal to approximately that of the largest yellowfin tuna on scientifically valid record--182 kg (Sharp, personal communication).

#### F. Discussion

Our bioenergetic analysis suggests that small skipjack and yellowfin tunas are growth-limited by food availability but that larger fish are growth-limited by their ability to consume and process available food. For each species, maximum observed body-weight corresponds approximately with that weight at which the maximum daily ration just fails to support a level of energy expenditure about twice that of the fish swimming at its minimum speed for hydrodynamic equilibrium.

Despite the qualitative similarity between species, there remains a striking quantitative difference: yellowfin tuna reach a maximum weight more than eight times that attained by skipjack tuna. Bioenergetically, the difference in maximum weights resolves itself principally as a difference in the weight exponents of metabolic rate. Specific metabolic rate of yellowfin tuna, presumably like that of typical fishes, is assumed to be proportional to  $W^{-0.2}$ ; whereas, metabolic rate of the skipjack seems nearly independent of weight (i.e.,  $M \propto W^0$ ). This difference, in turn, may reflect the presence and absence of a gas bladder in yellowfin and skipjack tunas, respectively. A gas bladder seems hydrodynamically obligatory for those tunas obtaining weights greater than 60 kg (Magnuson, 1973). The skipjack is among the largest of scombrids without a gas bladder. Absence of a gas bladder presumably enables skipjack to make vertical movements that are more rapid than those of which the yellowfin is capable. Thus, the skipjack would seem better adapted than yellowfin for exploitation of the epipelagic zone's vertical dimension, at least in terms of such speed-demanding activities as prey pursuit and predator avoidance.

For skipjack tuna, we have accounted for the unusual size-limiting role of maximum daily ration ( $C_{max}$ ) by suggesting that evolution of increased  $C_{max}$  was obviated by another, more inflexible, limit on maximum size--a size-progressive thermal squeeze, comprising convergence of the environmental temperature maximum for necessary dissipation of metabolic core heat with the minimum temperature (perhaps 15°C--see Dizon *et al.*, in press) for function of more peripheral tissues such as skin, gills, eyes, and brain. Can the thermal-squeeze argument also be made for yellowfin tuna? Perhaps so, but with less confidence than for the skipjack. The yellowfin tuna (a) appears capable of substantial physiological thermoregulation on a

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short-term basis (Dizon, recent unpublished data); and (b) exhibits a marked reduction in swimming speed--and presumably in metabolic rate--with decline in temperature ( $Q_{10} \sim 2$ --Dizon et al., in press). Therefore, the yellowfin tuna may not be subject to risk of overheating as it grows to maximum size.

It seems paradoxical that food availability should fail to be growth-limiting for large tunas, given that they live in what surely must be one of the most unproductive environments inhabited by fishes--the epipelagic zone of tropical seas. Reid (1962) indicates that broad regions of the central Pacific Ocean contain average net-zooplankton densities on the order of 25 parts per *billion* or less. Adult tunas feed at least one trophic level higher than net-zooplankton; thus, water with 25 ppb net-zooplankton might contain only about 2.5 ppb of tuna forage. That large tunas even survive in such a food-dilute environment--let alone obtain maximum daily rations--must testify both to the high degree of patchiness in distribution of tuna-forage and to a remarkable ability of tunas to locate and harvest aggregations of forage.

In conclusion, we suggest that the energetic limitations of skipjack, yellowfin, and, perhaps, most other tunas vary as a function of body size. Growth rates in small fish appear largely limited by food resources. Reduced growth rates in large fish may, in part, be due to increasing limitations of food-resource availability but more probably are due to the physiological limits imposed by adaptations which make tunas very efficient predators.

Evaluation of our hypotheses can be achieved by directly determining rates of feeding and/or metabolism in wild tunas. Because the former seems least logistically feasible, we recommend the latter. Laboratory studies could be employed to calibrate an ultrasonic telemetry system that monitors body-temperature differentials. If applied in conjunction with high-seas tracking of tunas, such an approach would provide an unique opportunity to determine actual habitat-activity level interactions for a free-swimming fish and, ultimately, the kinds of information that would allow a quantum increase in knowledge of tuna biology.

#### *Acknowledgments*

We thank Gary Sharp and Roy A. Stein, Jr., for review comments on an earlier draft of the manuscript. Partial support for the study was provided through contract funds from National Marine Fisheries Service, NOAA, to the University of Wisconsin.

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